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ARTICLE

A REVIEW OF SMALL-BODIED THEROPOD DINOSAURS FROM THE UPPER CRETACEOUS OF INDIA, WITH DESCRIPTION OF NEW CRANIAL REMAINS OF A NOASAURID (THEROPODA: ABELISAURIA)

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ABSTRACT—Small-bodied theropod dinosaurs are rare on southern landmasses but have been known from India for a century. Excavations by Charles Matley and Durgansankar Bhattacharji in uppermost Cretaceous sediments at Bara Simla, central India in 1917–1919 recovered small theropod vertebral and limb elements originally interpreted as coelurosaurians and separated into at least three species (*Compsosuchus solus*, *Laevisuchus indicus*, *Jubbulpuria tenuis*) based on features that can now be attributed to their serial position in the vertebral column. The comparatively recent discoveries of *Noasaurus leali* and *Masiakasaurus knopfleri* from similar-aged rocks in South America and Madagascar, respectively, and advances in basal theropod systematics led to a revised interpretation of most small-bodied Indian theropods as noasaurid abelisauroids. Here we review and redescribe *Laevisuchus*, *Jubbulpuria*, and *Compsosuchus*, including several elements that until now were thought lost, and describe a new partial noasaurid dentary from central India. The dentary bears the characteristic procumbent dentition of *Masiakasaurus*, which apparently is absent in *Noasaurus*. Likewise, cervical vertebrae of *Laevisuchus* more closely resemble those of *Masiakasaurus* than those of *Noasaurus*. Despite these similarities, phylogenetic analyses indicate that the balance of character data supports the Indian noasaurid species outside the sister-taxon pairing of South American and Malagasy species. Bones of small-bodied theropods have been recovered exclusively from the youngest Mesozoic localities in India (e.g., Pisdura, Bara Simla); to date they have not been reported from the slightly older localities in western and central India, from southern Indian sites in the Cauvery Basin, nor from the Vitakri Formation of Pakistan.

SUPPLEMENTARY FILES—Supplementary files are available for this article for free at www.tandfonline.com/UJVP.

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INTRODUCTION

The first reported discovery of dinosaur bones from the Indian Subcontinent dates back to 1828, when British Army Captain W. H. Sleeman (1844) recovered caudal vertebrae with notable ball-and-socket joints from Upper Cretaceous sediments at Bara Simla, located in "Jubbulpore" (now Jabalpur; Fig. 1). At that time, the name "Dinosauria" had not yet been coined, but the original triumvirate of genera that would later bear that name were already described (Buckland, 1824; Mantell, 1825, 1833). The Bara Simla dinosaur was later named "*Titanosaurus indicus*," distinguished by the shape and polarity of those ball-and-socket joints (Lydekker, 1877). It would remain India's only dinosaur genus for nearly half a century, until Charles Matley and Dhurgansankar Bhattacharji restarted excavations at Jabalpur and discovered the theropod *Lametasaurus indicus* (Matley, 1921, 1924). Numerous other discoveries in the early 20th century at Bara Simla, the neighboring locality Chhota Simla, and near the village of Pisdura provided the source materials for 18 of the 28 named dinosaur species from India (Chakravarti, 1934; Das-Gupta, 1930; Huene & Matley, 1933; Lydekker, 1879; see Carrano et al., 2011).

A second pulse of Cretaceous dinosaur discoveries in post-colonial India brought to light the partial skeleton of the titanosaur "*Titanosaurus*" *colberti* near Dongargaon, central India (Fig. 1; Berman & Jain, 1982; Jain & Bandyopadhyay, 1997) and of a rich field of dinosaur eggs and bones near Rahioli, western India (Chatterjee & Rudra, 1996; Dwivedi et al., 1982; Mathur & Pant, 1986; Mathur & Srivastava, 1987; Mohabey, 1983, 1984, 1987, 1989, 2001a; Mohabey et al., 2013; Srivastava et al., 1986). More recently, exploration in penecontemporaneous rocks of the Vitakri Formation in Balochistan, Pakistan has provided an additional source for dinosaur remains from the Indian subcontinent (Malkani et al., 2001; Malkani, 2004, 2006, 2015, 2020, 2021; Wilson et al., 2005).

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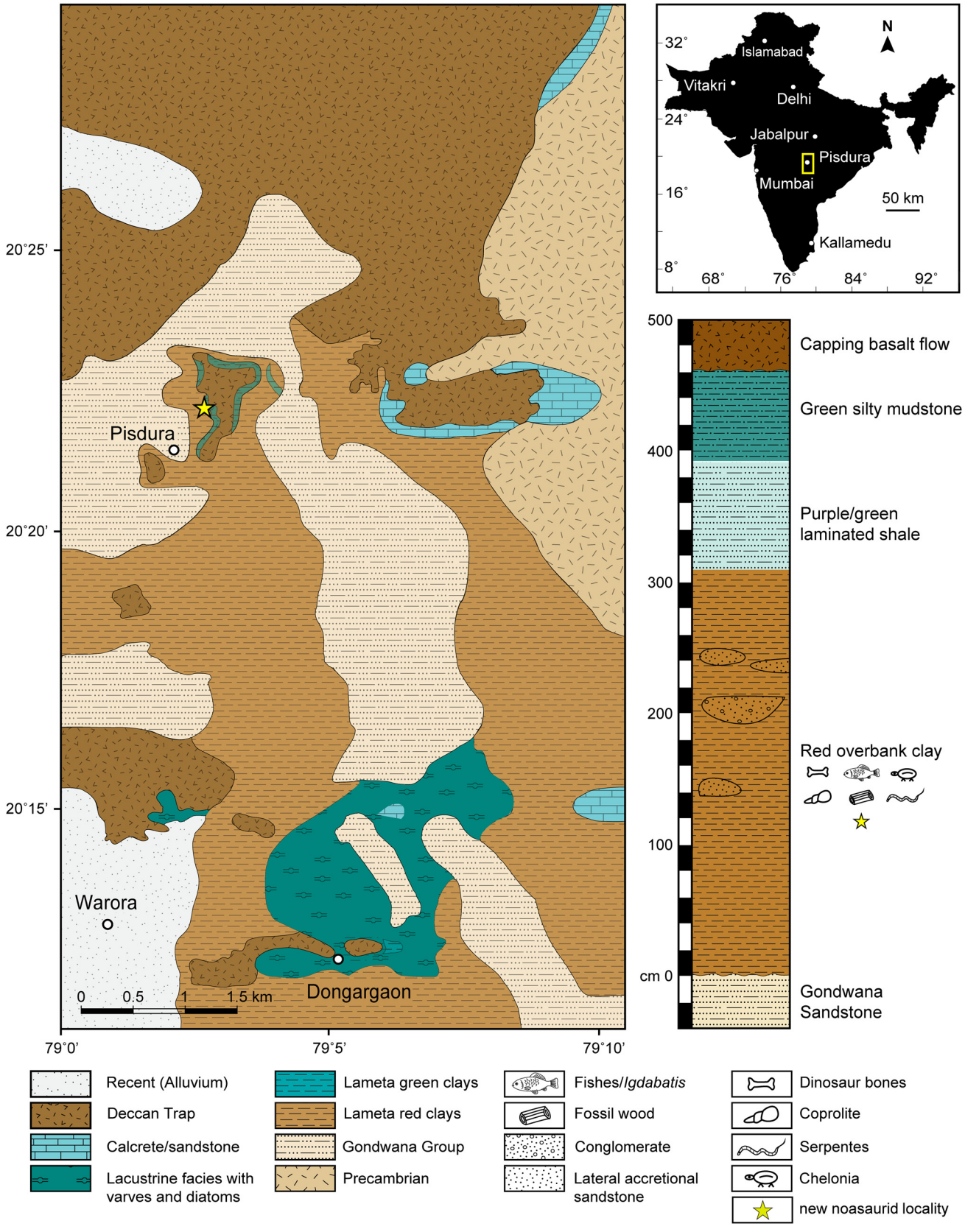

FIGURE 1. Geological map and stratigraphic section indicating the position of the Pisdura locality, from which the noasaurid dentary was collected. Inset map of Indo-Pakistan shows noasaurid localities at Jabalpur and Pisdura. Stratigraphic section at right is based on field reconnaissance by DMM and BS.

The vast majority of the hundreds of dinosaur bones that are known from the Lameta and Vitakri formations pertain to medium- and large-bodied species, which are interpreted as abelisaurid theropods (Bonaparte, 1991; Bonaparte & Novas, 1985) and titanosaur sauropods (Huene & Matley, 1933; Lydekker, 1877; Malkani et al., 2001). To date, very few bones pertaining to small-bodied dinosaur species (body length <5 m) have been reported, nearly all of which are vertebrae from the Bara Simla locality collected by Matley and Bhattacharji. Huene and Matley (1933) parsed these vertebrae into four species within Coelurosauria, apparently based on differences that are now viewed as attributable to their position in the vertebral column (see below). A single axis with fused axial intercentrum is the type and only specimen of *Compsosuchus solus*, three cervical vertebrae and a dorsal vertebra are the type series of *Laevisuchus indicus*, two caudal vertebrae are the type series of *Jubbulpuria tenuis*, and four caudal vertebrae are the type series of *Ornithomimoides*? *barasimlensis* (Huene & Matley, 1933:60–61, 64). Although several of these elements and parts of others are now lost (see Mohabey et al., 2013), sufficient material remains to evaluate the validity of each small-bodied theropod species, which Huene and Matley (1933) classified as compsognathid (*Compsosuchus solus*), "coelurid" (*Laevisuchus indicus*, *Jubbulpuria tenuis*), and ornithomimid (*Ornithomimoides*? *barasimlensis*) coelurosaurs.

Key insights into the affinities of these small-bodied Indian theropod species followed discoveries on other southern landmasses, particularly the Late Cretaceous of Argentina (*Noasaurus leali*, Bonaparte & Powell, 1980) and Madagascar (*Masiakasaurus knopfleri*, Sampson et al., 2001). Novas and Bandyopadhyay (1999, 2001) determined *Laevisuchus* to be a small abelisaurid and identified abelisaurid features in *Jubbulpuria*, *Compsosuchus*, and *Ornithomimoides*. Notably, they did not place those taxa within Noasauridae nor within the more inclusive clades Abelisauroidea (Bonaparte, 1991) or Abelisauria (Novas, 1992). Carrano et al. (2002) were the first to place *Laevisuchus* within Noasauridae, based on features of the cervical neural arch, a result backed up in subsequent phylogenetic analyses (Carrano & Sampson, 2008; Carrano et al., 2011).

Here we revise small-bodied theropod species from India and report on a partial dentary recently collected from Lameta Formation exposures near the village of Pisdura (Fig. 1). The new dentary specimen represents the first cranial remains of a small theropod species from the Indian Subcontinent and likely pertains to a noasaurid, possibly *Laevisuchus indicus* or a closely related taxon.

MATERIALS AND METHODS

Fossil Materials

The fossil dentary described in this contribution was mechanically prepared at the University of Michigan Museum of Paleontology using a micro-airscribe. The element was then molded and cast. The original specimens are housed at Rashtrasant Tukadoji Maharaj Nagpur University in Nagpur, India; casts are available at the University of Michigan Museum of Paleontology.

Micro-computed tomographic (μCT) scans were performed at the CTEES facility at the University of Michigan, Ann Arbor, MI, U.S.A., using a Nikon XT H 225 ST with a 0.1-mm-thick copper filter. The scanner is equipped with a tungsten target and was autoconditioned to maximum capacity at 225 kV. Scan settings were as follows: voltage = 136 kV; current =155 μA; exposure time = 1 s; projections = 3142; frames captured/projection = 2; flux normalization = enabled; ring artifacts = minimized. Uniform cubic voxels were 28 μm on a side.

We reconstructed the resulting scans using CT Pro 3D and saved the reconstructions as volume files. Three-dimensional visualization of the reconstructed data was performed using Mimics image processing software (Materialize NV). TIFF stacks are available from University of Michigan Deep Blue Data (https://doi.org/10.7302/1f9q-9a65).

Phylogenetic Analyses

The evolutionary relationships of the Indian theropod species discussed in this analysis were assessed using a modified version of a matrix published in the description of *Spectrovenator* by Zaher et al. (2020), which is itself based on earlier analyses by Pol and Rauhut (2012) and Rauhut and Carrano (2016). The revised *Spectrovenator* dataset includes 38 operational taxonomic units (OTUs) and 220 characters. We analyzed OTUs under equally weighted parsimony using TNT v.1.6 (Goloboff & Morales, 2023; Goloboff et al., 2008a, b), implementing a traditional heuristic search of 1,000 replicates of Wagner trees followed by tree bisection and reconnection branch swapping (10 trees saved per replication). All characters were unordered, equally weighted, and non-additive. *Herrerasaurus* was designated as the outgroup. We used the iterPCR method (Pol & Escapa, 2009) to detect unstable taxa and reduce the number of most parsimonious trees (MPTs)—thereby increasing resolution of the strict consensus. The NEXUS file used in the analysis is available as Supplementary File 2. The most parsimonious trees are available as Supplementary File 3.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, New York, U.S.A. **CCG**, Chengdu University of Technology, Chengdu, China; **FMNH**, Field Museum of Natural History, Chicago, IL, U.S.A.; **GSI**, Geological Survey of India, Kolkata (Calcutta), West Bengal, India; **MNN**, Musée National du Niger, Niamey, Niger; **RTMNU**, Rashtrasant Tukadoji Maharaj Nagpur University, Maharashtra, India; **UA**, Université d'Antananarivo, Madagascar; **UMMP**, University of Michigan Museum of Paleontology, Ann Arbor, MI, U.S.A; **USNM**, United States National Museum, Washington, DC, U.S.A.

SMALL THEROPODS FROM THE INDIAN SUBCONTINENT

Small-bodied theropod remains from the Indian subcontinent include numerous species that were collected from central India in the early 20th century, as well as remains more recently collected from southern India. Thus far, no small-bodied theropod remains have been reported from otherwise prolific localities in western India or Pakistan. We provide descriptions and photographs of specimens in "Systematic Paleontology."

Bara Simla, Jabalpur

Huene and Matley (1933) described nine new theropod species within eight new genera based on "thirty-two boxes of material" collected from the "Carnosaur Bed" at Bara Simla in Jabalpur (Fig. 1; Matley, 1924:105). Although all the theropod materials at Bara Simla were collected from a fairly restricted area "20 square yards in extent," the bones were "heaped together in this small space, with little regard to their original relationship" (Huene & Matley, 1933:3). Matley stated that the position of the bones in the "Carnosaur Bed" was documented during excavation (Huene & Matley, 1933), but these notes, if they still exist, have not yet been located in the archives of the Geological Survey of India. Elements from the "Carnosaur Bed" were divided into two "carnosaur" species and seven "coelurosaurian" species, based on "type"—that is, their morphological attributes (Huene & Matley, 1933:60).

Ironically, although the bulk of the small-bodied theropod material from Bara Simla was classified initially within

Coelurosauria, thus far none of the fossil bones from there or elsewhere in the Indian subcontinent can be confidently attributed to that clade (see below). Likewise, none of the numerous Late Cretaceous eggshell localities has produced a definitive avian oospecies (DMM, pers. observ.). The earliest-recorded coelurosaurian dinosaurs from India are the birds *Vastanavis* and *Quercypsitta* from the early Eocene (ca. 52 Ma) Cambay Formation (e.g., Mayr et al., 2007, 2010). The presence of fossil birds in the Late Cretaceous of Madagascar (Forster et al., 1996), however, suggests their absence from Mesozoic deposits of India is likely due to incomplete sampling.

In the only review of the Indian Museum collection since Huene and Matley's (1933) seminal work, Novas et al. (2004) judged *Compsosuchus solus* and *Jubbulpuria tenuis* to be nomina dubia but deemed *Laevisuchus indicus* a valid taxon. Carrano et al. (2011) suggested that if the Lameta fauna of India is similar to the Maeverano fauna of Madagascar, then *Compsosuchus*, *Jubbulpuria*, and *Laevisuchus* may all represent the same taxon.

Cauvery Basin

Dinosaur fossils were reported from the Cauvery Basin of southern India before notices of discoveries from central India made their way into the scientific literature. Blanford (1862:128, 139–140) reported remains of a tooth, which he referred to *Megalosaurus*, as well as bones that, although numerous, were "so saturated with water and so very friable, that it is impossible, even with the greatest care, to extract them in anything like a recognizable condition." Indeed, poor preservation of bones from the Kallamedu Formation (Ariyalur Group) has limited inferences into the diversity and faunal relationships of dinosaurs from southern India, which are thought to be roughly coeval with those of central and western India based on data from planktonic foraminiferans (see Prasad et al., 2013). As a result, only two dinosaur species have been named from the Kallamedu Formation, *Dravidosaurus blanfordi* and *Bruhathkayosaurus matleyi* (Yadagiri & Ayyasami, 1979, 1987). Both these species are based on fragmentary remains and have been the subject of taxonomic controversy. *Dravidosaurus* was initially interpreted as a stegosaur, but there is no evidence to support that hypothesis (e.g., Chatterjee & Rudra, 1996; Maidment, 2008; Wilson et al., 2011a). Several of the original bones attributed to *Dravidosaurus* are no longer available at the Geological Survey of India (Southern Region) collections (JAWM, pers. observ.), and one of the purported dermal plates assigned to the species has been reinterpreted as a weathered sauropod element (Galton & Ayyasami, 2017)—a determination that itself is only weakly supported. Likewise, the validity and affinity of *Bruhathkayosaurus* has been controversial. Upchurch et al. (2004) regarded it as an indeterminate sauropod. Pal and Ayyasami (2023: fig. 2) published field photographs of one of the original elements of *Bruhathkayosaurus*, which they suggest is a titanosaur tibia, but this new information has not resolved the identity of the element nor the validity of the taxon. Despite this grave uncertainty, it has been speculated that the individual of *Bruhathkayosaurus* represents the largest known land animal (Paul & Larramendi, 2023).

More recent exploration in the Cauvery Basin has brought to light more diagnostic remains from north of the town of Kallamedu (Fig. 1), including definitive notosuchian and theropod teeth (Goswami et al., 2013; Prasad et al., 2013). The notosuchian tooth was found to be closest in form to the Malagasy form *Simosuchus*, and among the theropod teeth collected was a single specimen considered to be "the first Gondwanan record for troodontids, extending their geographic range by nearly 10,000 km … an unexpected and distinctly 'Laurasian' component of an otherwise typical 'Gondwanan' tetrapod assemblage" (Goswami et al., 2013:1). This pairing is indeed unexpected, and the hypothesized troodontid features (i.e., presence of a lingual buttress and a basal constriction of the crown, the shape of the crown in labial view, and the shape of the apically oriented denticles) await testing in a quantitative phylogenetic framework. The uncertainty surrounding the content of the dinosaur fauna of the Kallamedu Formation—as well as that of the Indian Subcontinent in general—does admit the possibility for aberrant forms, such as troodontids, but morphological variation within already recorded taxa is poorly known. For example, teeth are only known for two of the five valid theropod species already recorded in India (Wilson et al., 2011a) (Table 1). And for those two species there is almost no understanding of either serial or ontogenetic variation in tooth shape, and it is extremely difficult to differentiate a tooth from a small-bodied species from that of a small individual (or replacement tooth) of a larger-bodied species. The Malagasy taxa *Majungasaurus* and *Masiakasaurus* are much more completely known than any Indian taxon, but serial and ontogenetic variation are only adequately known in the former (e.g., Smith, 2007); posterior maxillary or dentary teeth are not known yet for *Masiakasaurus* (Carrano et al., 2002, 2011). For these reasons, we consider the Kallamedu theropod tooth to be Neotheropoda incertae sedis pending further evidence.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
THEROPODA Marsh, 1881
CERATOSAURIA Marsh, 1884
ABELISAUROIDEA Bonaparte, 1991
NOASAURIDAE Bonaparte and Powell, 1980
LAEVISUCHUS INDICUS Huene in Huene and Matley, 1933
(Figs. 2–6)

Lectotype—We designate a nearly complete mid-cervical vertebra, GSI K27/696, as the lectotype of *Laevisuchus indicus* (Huene & Matley, 1933:60–61; pl. 20, fig. 3).

Referred Specimens—The three other vertebrae in the original type series of *Laevisuchus indicus*, cervical vertebrae GSI K20/614 and GSI K20/613 and dorsal vertebra GSI K27/588 (Huene & Matley, 1933: 60–61; pl. 20, figs. 2, 4, 5), appear to belong to the same species as the lectotype, but there is not yet definitive evidence they belong to the same individual—although

TABLE 1. Measurements of the anterior dentary fragment (RTMNU/DG/VERT/1/55P/2020) in millimeters. The nutrient groove and Meckelian groove were used as proxies for establishing the horizontal. 'Long axis' and 'short axis' were used for alveolar measurements in place of 'mesiodistal length' and 'transverse breadth' because the tooth sockets are rotated slightly outwards with respect to the long axis of the dentary.

Dimension	Measurement
Length	47.1
Height	24.2
Breadth	12.4
Alveolus 1, long axis	6.1
Alveolus 1, short axis	5.0
Alveolus 2, long axis	6.6
Alveolus 2, short axis	5.8
Alveolus 3, long axis	7.4
Alveolus 3, short axis	6.5
Alveolus 4, long axis	9.0
Alveolus 4, short axis	6.4
Alveolus 5, long axis	—
Alveolus 5, short axis	6.6

that is a possibility. One of these elements, cervical vertebra GSI K20/614, is currently missing from the collections of the Geological Survey of India. Unfortunately, it was only figured in ventral view (Huene & Matley, 1933:pl. 20, fig. 4) and received no description.

Two caudal vertebrae (GSI K20/612, GSI K27/614), originally in the type series of *Jubbulpuria tenuis*, very likely pertain to *Laevisuchus indicus*. These two vertebrae were initially identified by Huene and Matley (1933:61) as dorsal vertebrae with thin-walled centra that were distinguished from *Laevisuchus* by their narrow diapophyses that lack "indications of buttresses [laminae]." Those vertebrae are now interpreted to be caudal vertebrae (e.g., Carrano et al., 2011; Novas et al., 2004), removing the features that distinguish them from *Laevisuchus* and opening the possibility that they represent the same species. There are very few serially homologous features that can be compared between the presacral vertebrae of the *Laevisuchus indicus* type series and the caudal vertebrae of the *Jubbulpuria tenuis* type series, but they are all delicate in form and the centra are thin-walled—as their original generic and specific names, respectively, suggest. The size of the centrum of these three cervical, one dorsal, and two caudal vertebrae is consistent with them pertaining to the same individual, based on comparisons with an associated individual of *Masiakasaurus knopfleri* (Carrano et al., 2011:table 1). Mid-cervical centrum GSI K27/696 is 4.5 cm long, dorsal centrum K27/588 is 3.5 cm long, and distal caudal centra K27/614 and K20/612 are 4.7 cm and 4.1 cm long, respectively. Based on their similar morphology, consistent size, lack of duplication, and provenance within a fairly restricted area of the "Carnosaur Bed" we suggest they all belong to the same species. We retain the name *Laevisuchus indicus*, which appears first in the monograph of Huene and Matley (1933:60, 61), and subsume *Jubbulpuria tenuis* within that species.

Locality and Horizon—The lectotype and referred remains of *L. indicus* were collected from the "Carnosaur Bed" at Bara Simla, Madhya Pradesh, central India. The "Carnosaur Bed" is a small, localized deposit of the Lameta Formation intercalated between the "Green Sand" and "Main Limestone" layers (see Huene & Matley, 1933:fig. 1; Matley, 1921). The Lameta Formation is regarded as latest Cretaceous in age, based on its relationship to overlying basalts that were deposited during magnetochron C29R (Hansen et al., 2005). The C29R Lameta Formation exposures at Bara Simla are slightly younger than the transitional C30N-C29R deposits at Dongargaon, which themselves are younger than the C30N deposits at Rahioli (Wilson Mantilla et al., 2022).

Comments— *Laevisuchus indicus* was described based on four vertebrae, originally interpreted as pertaining to the cervical (GSI K20/614, GSI K20/613, GSI K27/696) and dorsal (GSI K27/588) series (Huene & Matley, 1933:60–61; pl. 20, figs. 2–5). Because none of these were declared to be the type, the four vertebrae constitute a type series. The nearly complete, well-preserved cervical vertebra GSI K27/696 has acted as the de facto type of *Laevisuchus indicus*, because it is the only element that has been adequately described and—until recently—was thought to be the only element available in the Geological Survey of India collections (e.g., Carrano et al., 2011; Novas et al., 2004). One of the three vertebrae presumed to be missing, GSI K20/613, was rediscovered as isolated pieces placed in separate boxes (Mohabey et al., 2013:fig. 3B). The pieces are now rejoined, and it appears that only a portion of the right prezygapophysis is missing, based on what can be compared with the original illustrations (Huene & Matley, 1933:pl. 20., fig. 2). A portion of another of the missing vertebrae, GSI K27/588, also was recently rediscovered in collections of the Geological Survey of India (Mohabey et al., 2013). It now lacks most of the neural arch and some parts of the margin of the centrum articular faces. Cervical vertebra GSI K20/614 remains missing; it was not described and only figured in one view (see Huene & Matley, 1933:pl. 20, fig. 4). We selected GSI K27/696 to be the *Laevisuchus indicus* lectotype because it is the most complete and best preserved of the type series, which cannot be demonstrated to represent a single individual.

Novas et al. (2004:80–81) regarded *Laevisuchus indicus* a valid taxon, but they did not identify autapomorphies supporting that assessment. Likewise, Carrano and Sampson (2008:13) listed no diagnostic features of *Laevisuchus indicus* but nonetheless regarded it as a valid species due to its unique spatiotemporal distribution.

Revised Diagnosis— *Laevisuchus indicus* can be differentiated from *Noasaurus* and *Masiakasaurus* by pre- and postzygapophyses that have blunted anterior points flanked by a gentle medial concavity and by its anteroposteriorly abbreviate proportions (Fig. 2A). The neural spine in *L. indicus* is positioned near the center of the trapezoid formed by the zygapophyses in dorsal view (Fig. 2A); in *Masiakasaurus* it is shifted forward of center. The neural spine is not well enough preserved in *Noasaurus* to determine its position. *Laevisuchus indicus* differs from *Noasaurus* by having an anteriorly broadening neural arch in dorsal view and more deeply incised spinopostzygapophyseal laminae that expose the centrum in dorsal view (Fig. 2A).

Description—*Laevisuchus* vertebra GSI K27/696 represents a mid-cervical vertebra, possibly the sixth, based on comparisons with *Masiakasaurus* by Carrano et al. (2011:16). Novas et al. (2004) suggested it could be the fifth cervical vertebra without further comment. The vertebra is beautifully preserved and provides the richest source of character data for *Laevisuchus* in the GSI collections (Fig. 2). Sometime after publication of the Huene and Matley (1933) memoir, GSI K27/696 was broken at the neurocentral junction and re-joined incorrectly, with the neural arch and centrum oriented in opposite directions (see, for example Carrano et al., 2002: fig. 7). This vertebra has since been repaired by the authors with permission from the Curatorial Division of the Geological Survey of India. The vertebra is nearly complete, lacking only tips of both diapophyses, the epipophyses, and the left parapophysis.

The centrum and neural arch are subequal in height, but the neural arch is significantly broader transversely and longer anteroposteriorly (Fig. 2B, C). As a result, the vertebra appears top-heavy. The centrum is slightly elongate, with an average elongation index of 1.5 (aEI; Chure et al., 2010). The centrum articular surfaces are asymmetrical; the posterior face is 1.4 times broader transversely than it is tall dorsoventrally. The anterior face of the centrum is nearly flat, and the posterior face is slightly concave. A distinctive pattern of three pneumatopores open on the lateral aspect of the centrum (Fig. 2C, D). The lower two of these appear to enter the centrum and represent pleurocentral foramina, but the more dorsal, centrally positioned opening represents a pneumatopore in the centrodiapophyseal fossa. The centrum appears to be quite hollow internally, based on breaks in the anterior portion of the centrum in the region of the parapophysis (Fig. 2C). The ventral and lateral aspects of the centrum are relatively flat; they are separated by the gently rounded ventrolateral edge of the centrum. In ventral view, the centrum is transversely narrowest near mid-centrum (Fig. 2B). It expands anteriorly, beginning near the position of anteriormost pneumatopore. The parapophyses are prominent and flush with the anterior face of the centrum. The better preserved right parapophysis appears to be enlarged and slightly ventrally facing.

The neural arch forms a 'table' in dorsal view (sensu Welles, 1984) anchored by the zygapophyses and the anteroposteriorly directed epipophyseal-prezygapophyseal lamina (EPRL) between the pre- and postzygapophyses (Fig. 2A; Bonaparte 1996:90; Wilson, 2012; Wilson et al., 2011b). This zygodiapophyseal table expands anteriorly in dorsal view, so that the

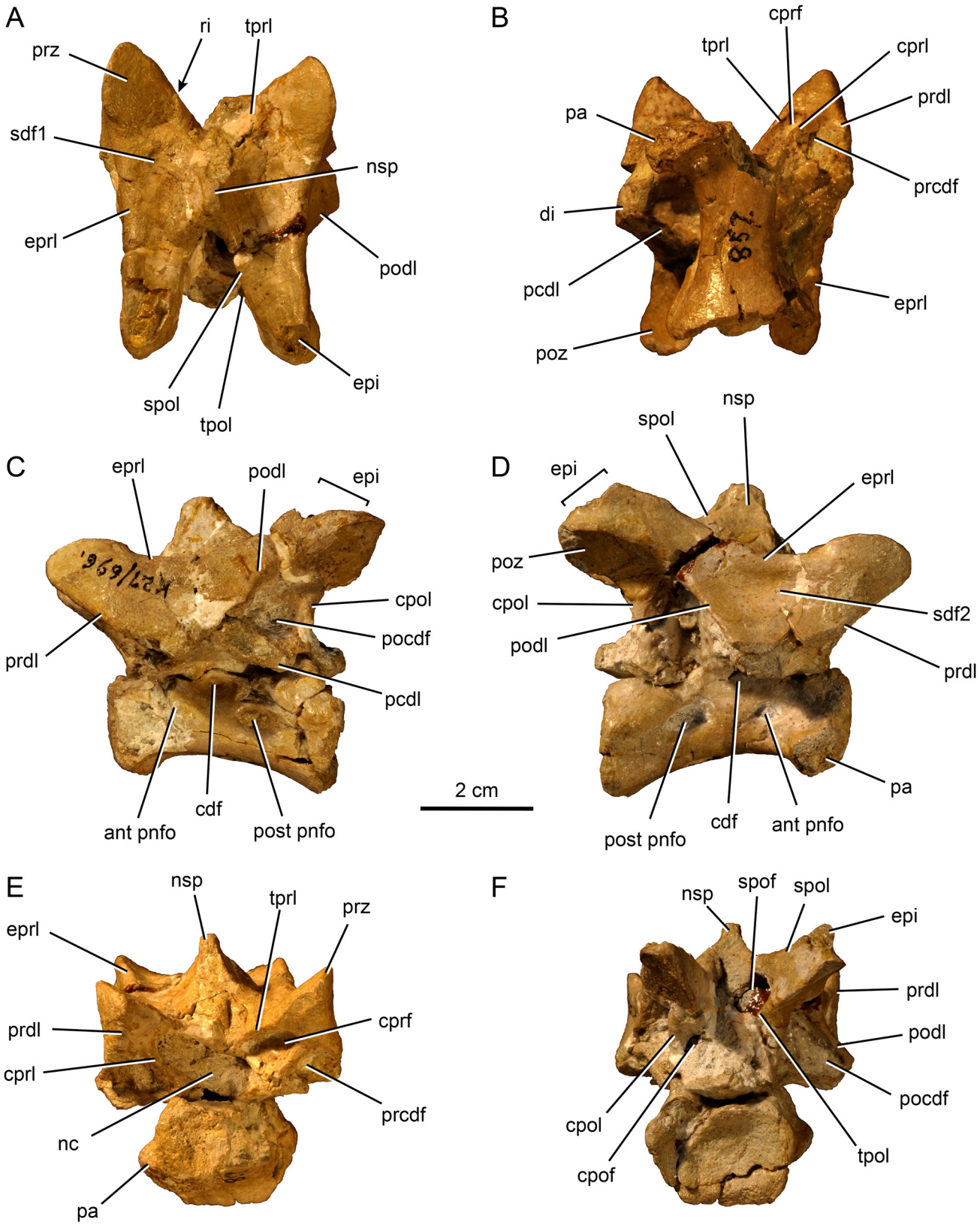

FIGURE 2. *Laevisuchus indicus* cervical vertebra GSI K27/696 in **A**, dorsal, **B**, ventral, **C**, left lateral, **D**, right lateral, **E**, anterior, and **F**, posterior views. **Abbreviations**: **ant**, anterior; **cdf**, centrodiapophyseal fossa; **cpof**, centropostzygapophyseal fossa; **cpol**, centropostzygapophyseal lamina; **cprf**, centroprezygapophyseal fossa; **cprl**, centroprezygapophyseal lamina; **di**, diapophysis; **epi**, epipophysis; **eprl**, epipophyseal-prezygapophyseal lamina; **nc**, neural canal; **nsp**, neural spine; **pa**, parapophysis; **pcdl**, posterior centrodiapophyseal lamina; **pnfo**, pneumatic foramen; **pocdf**, postzygapophyseal centrodiapophyseal fossa; **podl**, postzygodiapophyseal lamina; **post**, posterior; **poz**, postzygapophysis; **prcdf**, prezygapophyseal centrodiapophyseal fossa; **prdl**, prezygodiapophyseal lamina; **prz**, prezygapophysis; **ri**, ridge; **sdf**, spinodiapophyseal fossa; **spof**, spinopostzygapophyseal fossa; **spol**, spinopostzygapophyseal lamina; **tpol**, intrapostzygapophyseal lamina; **tprl**, intraprezygapophyseal lamina.

prezygapophyses are more broadly separated than are the postzygapophyses. This feature is serially variable, based on comparisons with *Masiakasaurus* (Carrano et al., 2002:fig. 7A). The neural spine is at the geometric center of the trapezoid formed by the zygapophyses; it is areally restricted and rectangular in dorsal view, being approximately twice as long anteroposteriorly as it is broad transversely. In lateral view, the neural spine rises slightly above the level of the zygodiapophyseal table. There is a distinct break in curvature in the EPRL just anterior to the postzygapophysis.

Spinodiapophyseal fossae (SDF1, SDF 2) are present. They are oriented at right angles to one another and separated by the EPRL. SDF 1 is exposed on the dorsal aspect of the zygodiapophyseal table, and SDF 2 is exposed on the lateral aspect of the zygodiapophyseal table (Fig. 2A, D). The postzygapophyses connect to the neural spine via elongate spinopostzygapophyseal laminae (SPOLs). There is a notably deep notch separating the SPOLs, which exposes the dorsal aspect of the posterior centrum in dorsal view (Fig. 2A). In contrast, the spinoprezygapophyseal laminae (SPRLs) joining the prezygapophyses and neural spine are shorter and less prominent. A small spinopostzygophyseal fossa (SPOF) is present between the postzygapophyses and the neural spine, but there appears to be no complementary fossa developed above the prezygapophyses.

Both the prezygapophyses and the postzygapophyses are characterized by uniquely shaped facets. They are suboval in shape and marked by a blunt anterior point accentuated by a medial concavity (Fig. 2A). The prezygapophyseal facet bears a raised lip on its posteromedial margin; this may have acted as an anatomical 'stop' to resist translation in that direction. Pneumatic fossae below the zygapophyses are well developed. A deep centroprezygapophyseal fossa (CPRF) is present between the intraprezygapophyseal and centroprezygapophyseal laminae (TPRL, CPRL). On the more completely prepared left side, two pneumatic foramina are visible within the CPRF. Lateral to the CPRF is a pneumatic fossa between the CPRL, anterior centrodiapophyseal lamina (ACDL), and prezygodiapophyseal lamina (PRDL). It too bears a pneumatic foramen within it. Just posterior to the CPRF on the lateral aspect of the centrum is a postzygapophyseal centrodiapophyseal fossa (POCDF) between the posterior centrodiapophyseal lamina (PCDL), postzygodiapophyseal lamina (PODL), and centropostzygapophyseal lamina (CPOL).

Referred cervical vertebra GSI K27/613 (Fig. 3) and dorsal vertebra GSI K27/588 (Fig. 4) were much less complete than the lectotypic specimen GSI K27/696 when they were originally described, and damage has exaggerated this difference. GSI K27/613 is the more complete of the two referred specimens, consisting of a partial neural arch and centrum. Based on comparisons with figures in the original description, GSI K27/613 now lacks the right prezygapophyseal process and part of the left (Huene & Matley, 1933:pl. 20, fig. 2). Several important discrepancies are apparent between the specimen and the illustrations in Huene and Matley (1933). In dorsal view, there was no distinction made between the spinopostzygapophyseal laminae and the centrum, and as a result the angled incision between the SPOLs is not apparent (Fig. 3A; Huene & Matley, 1933:pl. 20, fig. 2b). In that same view, the right postzygapophysis and epipophysis were not portrayed, even though they are preserved. The left EPRL was not portrayed accurately, and the transverse expansion of the neural arch was not made apparent. The ventral view of the specimen is oriented with anterior facing down (rather than up, as is standard), and the preservation of the parapophyses is not accurately portrayed (Huene & Matley, 1933:pl. 20, fig. 2e). In most respects, vertebra GSI K27/613 resembles GSI K27/696. Its centrum is gracile and expands transversely both anteriorly and posteriorly. The neural arch is broader and longer than the centrum and trapezoidal in dorsal view. The prezygapophyses are more broadly separated than are the postzygapophyses. There is a deep notch between the SPOLs and development of SDF 1 and 2 on the dorsal and lateral aspect of the neural arch, respectively. Three pneumatic foramina are present on the lateral aspect of the centrum and base of the neural arch, corresponding to the pleurocentral foramina and pneumatopore within the centrodiapophyseal fossa, respectively. The sharp inflection in the EPRL near the postzygapophysis is not apparent in GSI K27/613, and it is not known whether there are pneumatopores within the CRPF and PRCDF, as there are in GSI K27/696.

As mentioned above, referred cervical vertebra GSI K20/614 is not currently available in collections, was only figured in ventral view, and received no description (Huene & Matley, 1933:pl. 20, fig. 4). In general terms it resembles GSI K27/696, but owing to preservation and lack of alternate views, many salient features cannot be evaluated. For example, it cannot be determined whether the neural arch is trapezoidal in dorsal view or whether pneumatic fossae were punctuated with pneumatic foramina. It does appear that at least the right prezygapophysis resembles the shape of GSI K27/696, and that both a PRCDF and POCDF are present.

Vertebra GSI K27/588 was originally described as a dorsal vertebra by Huene and Matley (1933:pl. 20, fig. 5). More recently, based on those illustrations Carrano et al. (2011:35) further specified its serial position as "the mid-dorsal region" based on the offset of its articular faces and the shape of the neural arch. As mentioned above, only the centrum and base of the neural arch remain of dorsal vertebra GSI K27/588 (Fig. 4). The margins of the centrum, particularly on its anterior face, have been damaged substantially since the original description. Like cervical vertebra GSI K27/696, the anterior centrum is nearly flat, and the posterior face is slightly concave. Carrano et al. (2011) noted the absence of a pneumatopore on the lateral aspect of the centrum, probably because this feature was left out of Huene and Matley's (1933) illustration and description. In fact, a conspicuous single pneumatopore is visible in left lateral view (Fig. 4C). Very little else can be said of this specimen.

Referred caudal vertebrae GSI K20/612 and GSI K27/614 (Figs. 5, 6), formerly set apart as "*Jubbulpuria tenuis*," are similar in shape and size and may represent the same individual, but at present there are no field data to support that hypothesis. The two vertebrae differ slightly in their apparent stoutness, with GSI K27/614 having a slightly greater centrum height-to-length ratio compared with GSI K20/612; this suggests it pertains to a slightly more proximal position in the tail. Caudal vertebra GSI K27/614 lacks the anterior portion of its centrum but preserves basal portions of its transverse process, the left postzygapophyses, and most of the neural spine. Caudal vertebra GSI K20/612 has a well-preserved centrum, but it lacks the distal portion of its transverse processes, both pre- and postzygapophyses, and its neural spine.

The centrum, which is best preserved in GSI K20/612, is an elongate, waisted cylinder whose length is more than twice its posterior height (42 × 18 mm; Fig. 6B). The anterior articular face is slightly taller than wide (18 × 16 mm), tapering to approximately one-third its breadth by mid-centrum (5 mm; Fig. 6E). Exemplar GSI K27/614 is much less waisted at mid-centrum, only tapering to approximately half its posterior breadth (Fig. 5B). Some of this difference may be accounted for relatively poor preservation of the anterior end of the centrum, as well as serial variation. The caudal centrum of GSI K20/612 is asymmetrically amphicoelous, with a nearly flat anterior face and a moderately concave posterior face (Fig. 6D, E). GSI K20/614 likewise bears a concave posterior

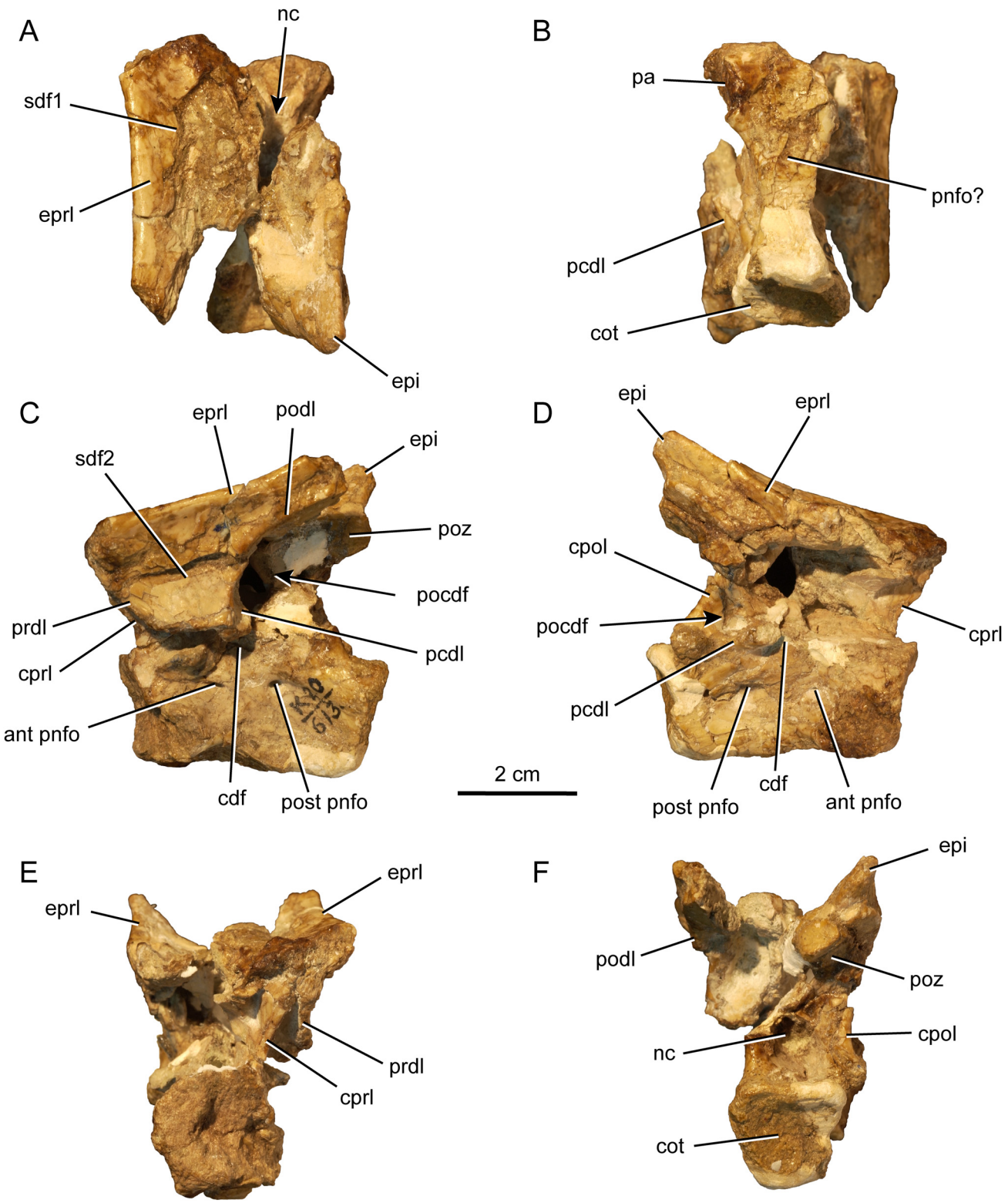

FIGURE 3. *Laevisuchus indicus* cervical vertebra GSI K27/613 in **A**, dorsal, **B**, ventral, **C**, left lateral, **D**, right lateral, **E**, anterior, and **F**, posterior views. **Abbreviations**: **ant**, anterior; **cdf**, centrodiapophyseal fossa; **cpol**, centropostzygapophyseal lamina; **cprl**, centroprezygapophyseal lamina; **cot**, cotyle; **epi**, epipophysis; **eprl**, epipophyseal-prezygapophyseal lamina; **nc**, neural canal; **pa**, parapophysis; **pcdl**, posterior centrodiapophyseal lamina; **pnfo**, pneumatic foramen; **pocdf**, postzygapophyseal centrodiapophyseal fossa; **podl**, postzygodiapophyseal lamina; **post**, posterior; **poz**, postzygapophysis; **prdl**, prezygodiapophyseal lamina; **sdf**, spinodiapophyseal fossa.

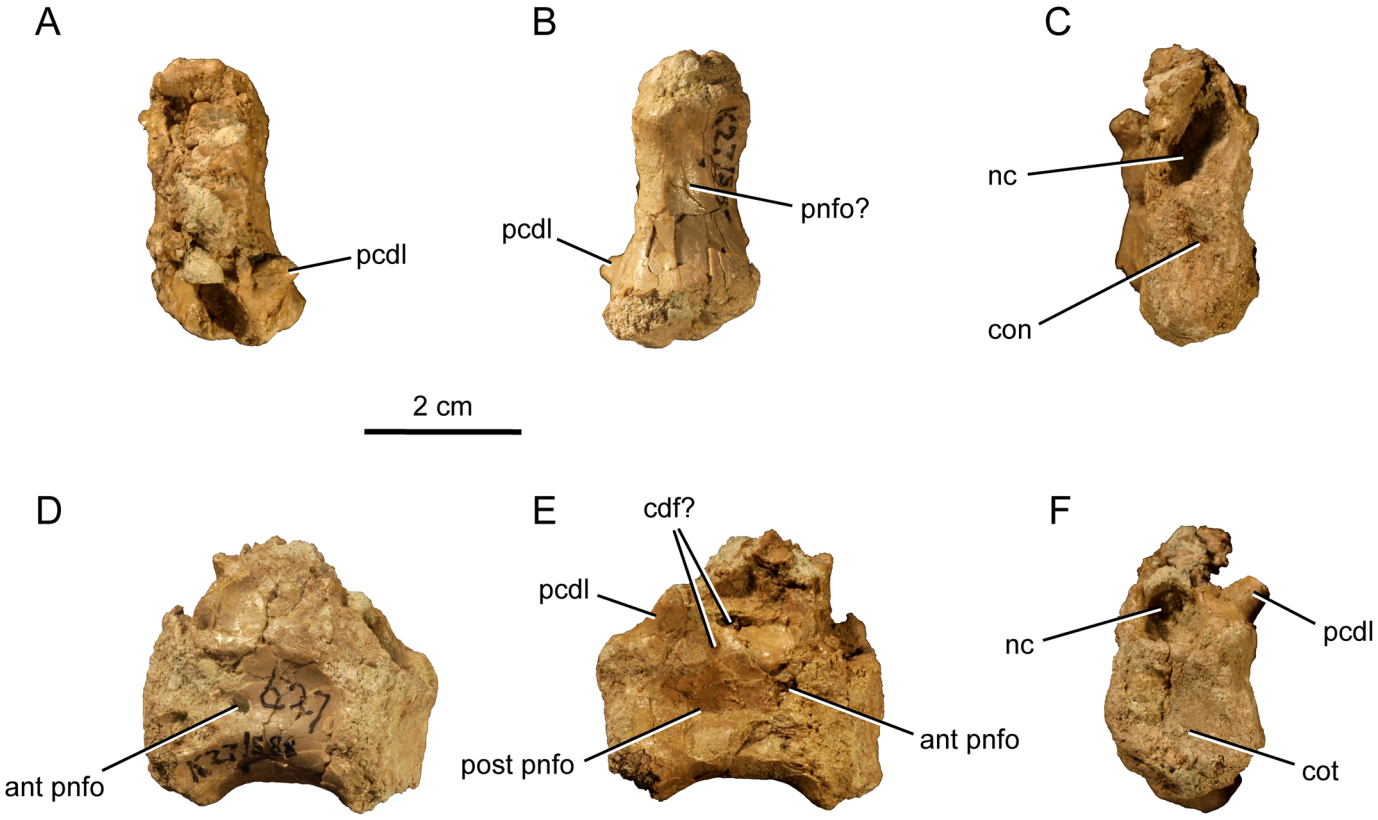

FIGURE 4. *Laevisuchus indicus* dorsal vertebra GSI K27/588 **A**, dorsal, **B**, ventral, **C**, anterior, **D**, left lateral, **E**, right lateral, and **F**, posterior views. **Abbreviations**: **ant**, anterior; **cdf**, centrodiapophyseal fossa; **con**, condyle; **cot**, cotyle; **nc**, neural canal; **pcdl**, posterior centrodiapophyseal lamina; **pnfo**, pneumatic foramen; **post**, posterior.

face. Its neural arch is approximately half the height of the centrum, and the postzygapophyses notably extend slightly beyond its posterior margin. The postzygapophyseal facets are nearly vertically oriented and elliptical in shape, with the long axis oriented in the same direction as the blunt, weakly developed postzygodiapophyseal lamina connecting the transverse process and postzygapophysis. A thin spinopostzygapophyseal lamina is also present, and together with the postzygodiapophyseal lamina it borders a shallow fossa on the lateral neural spine (Fig. 5C). This fossa is also preserved on GSI K20/612 (Fig. 6C). The neural spine is not completely preserved in GSI K27/614, but its footprint near the base of the neural arch appears to have been elongate anteroposteriorly. A small portion of the posterior neural spine is preserved on GSI K27/614 (Fig. 5A). It is slightly expanded transversely and appears to taper towards its preserved anterior margin. As preserved in the other exemplar, GSI K20/612, the neural spine extends as a narrow keel on the anterior portion of the neural arch. The transverse processes are partially preserved in both exemplars. They appear to be anteroposteriorly elongate structures that are deepest posteriorly. Specimen GSI K27/614 preserves the posterolateral portions of the left and right transverse processes to differing degrees. These indicate they are rounded and thick at their posterior extreme, tapering in thickness to a fine lamina by approximately centrum mid-length. The transverse processes would also taper in transverse breadth anteriorly; the sweep of that taper is captured on the right side of GSI K20/612. No infradiapophyseal laminae were preserved, but a conspicuous fossa is developed on the posterior transverse process near the base of the postzygodiapophyseal lamina.

We note here that additional small, gracile caudal vertebrae labeled "K20/612" are present in the as yet undescribed Matley collection in the Indian Museum (see Mohabey et al., 2013: 36). It is not clear what the relationship, if any, is among these small caudal vertebrae and the specimen described above. It is certain, though, that the element described above (Fig. 6) is the same as that described and figured by Huene and Matley (1933:pl. 20, fig. 6).

NOASAURIDAE Bonaparte and Powell, 1980
INDETERMINATE SPECIES
(Figs. 7–9)

Referred Specimen—RTMNU/DG/VERT/1/55P/2020, a partial right dentary preserving the first five alveoli with portions of functional or replacing teeth in each.

Locality and Horizon—The partial dentary was surface-collected from sediments of the Lameta Formation exposed near the village of Pisdura in eastern Maharashtra State, central India (Fig. 1). The locality (20°21′N, 79°2′E) is part of a farmer's field that brings up isolated bones from the overbank red clays when ploughed, a peculiar mode of occurrence taken advantage of by Matley (1921), Jain and Sahni (1983), and other researchers. The red clays have produced a series of snake vertebrae described as *Madtsoia pisdurensis* (Mohabey et al., 2011), pelomedusoid turtles, numerous incomplete bones of titanosaurs (Huene & Matley, 1933), and plant-bearing coprolites attributed to sauropods (Mohabey, 2001b; Prasad et al., 2005, 2011).

The Maastrichtian age for the Lameta Formation is supported by coccoliths (Salis & Saxena, 1998), magnetostratigraphy

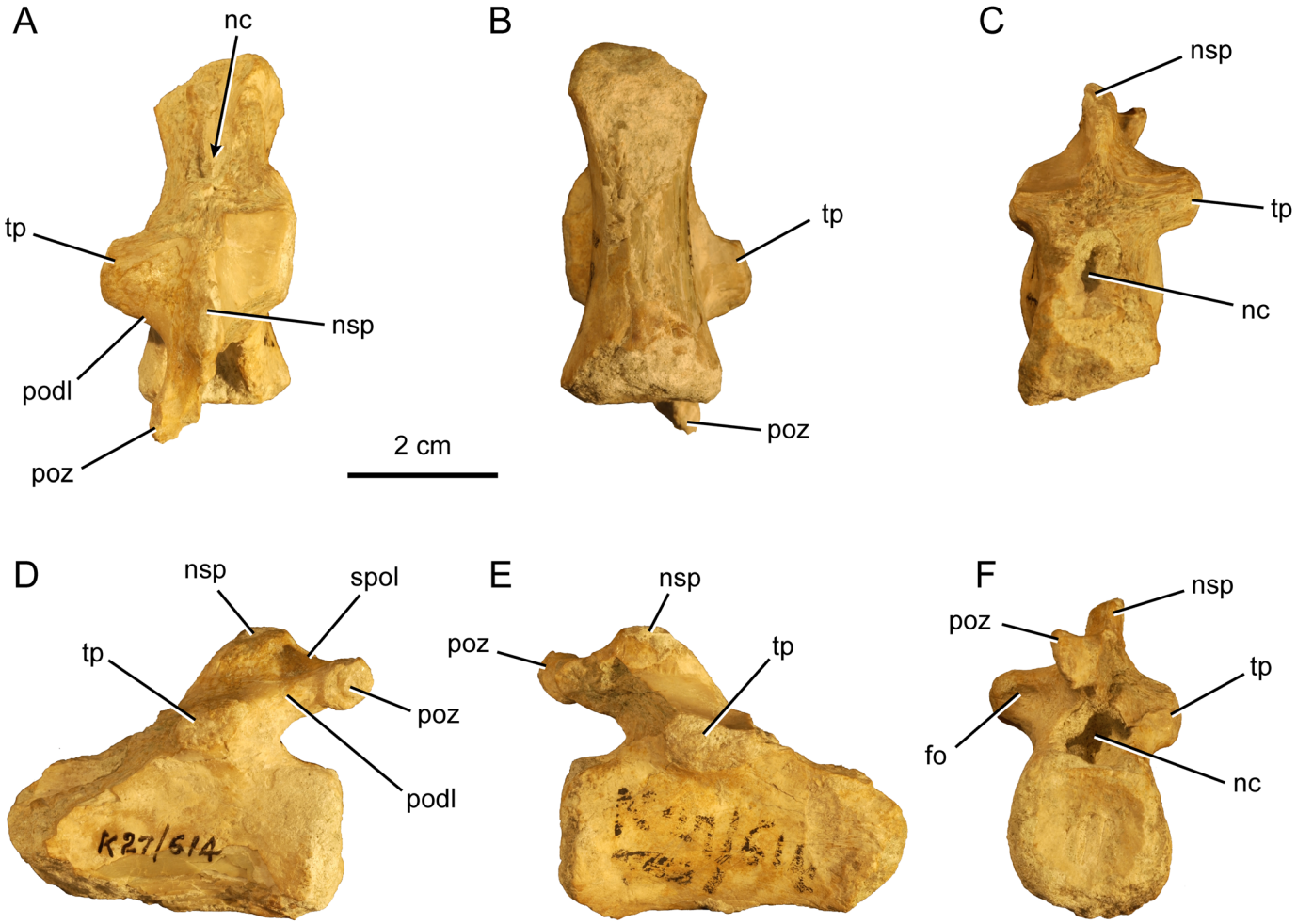

FIGURE 5. *Laevisuchus indicus* caudal vertebra GSI K27/614 in **A**, dorsal, **B**, ventral, **C**, anterior, **D**, left lateral, **E**, right lateral, and **F,** posterior views. **Abbreviations**: **fo**, fossa; **nc**, neural canal; **nsp**, neural spine; **podl**, postzygodiapophyseal lamina; **poz**, postzygapophysis; **spol**, spinopostzygapophyseal lamina; **tp**, transverse process.

indicating reversed polarity (C29r; Hansen et al., 2005), and palynostratigraphy (Samant & Mohabey, 2005). The flow overlying the bone-bearing horizon at Pisdura is younger than the flow overlying the Dongargaon locality; both flows are younger than those capping western Indian localities (e.g., Rahioli, Dholi Dungri), which have not yet been radiometrically dated but present normal magnetic polarity (magnetochron 30N; Mohabey & Samant, 2013).

Comments—The new partial dentary (RTMNU/DG/VERT/1/55P/2020) was not found in association with other elements, and so there is no anatomical overlap with other small-bodied theropod species from India, all of which are based on postcranial remains. As discussed below, the dentary preserves features shared by the noasaurid *Masiakasaurus* that suggest it likely pertains to a noasaurid. Whether RTMNU/DG/VERT/1/55P/2020 pertains to *Laevisuchus indicus* or to a closely related noasaurid species, diagnostic features are evident: dentary teeth are moderately procumbent, ranging from 47–23° across the first five teeth; serration density is approximately 7 serrations/mm.

Description—RTMNU/DG/VERT/1/55P/2020 is the anteriormost portion of a right dentary. Five alveoli are identifiable, and there are partial crowns present in the first, third, and fifth alveolus. All crowns are broken off flush with the preserved margin of the jaw. The ventral margin of the dentary is complete, but the alveolar margin and dorsal portion of the symphysis are not preserved. Surface details are well preserved on the medial and lateral sides of the dentary. Measurements of the dentary are provided in Tables 1 and S1. We used the orientation of the nutrient groove and the Meckelian groove as a proxy for the horizontal in Figures 7–9 and in the description below. Orientation of the dentary in the sagittal and coronal planes was based on alignment with the long axis passing through the tooth row and individual teeth, respectively.

The preserved portion of the dentary represents the anterior one-third of that element, based on comparisons with *Masiakasaurus* (Carrano et al., 2002:fig. 3). In medial view, the dentary is smooth and nearly featureless, with two distinct, parallel grooves directed anteroposteriorly (Fig. 7D). The more dorsally positioned of these is a nutrient groove that extends throughout the preserved length of the dentary. The more ventrally positioned of these is the Meckelian groove, which does not extend anteriorly beyond the fourth alveolus. The two grooves are similar in their dorsoventral height (ca. 2 mm) but differ in their depth, with the nutrient groove being much deeper (3–

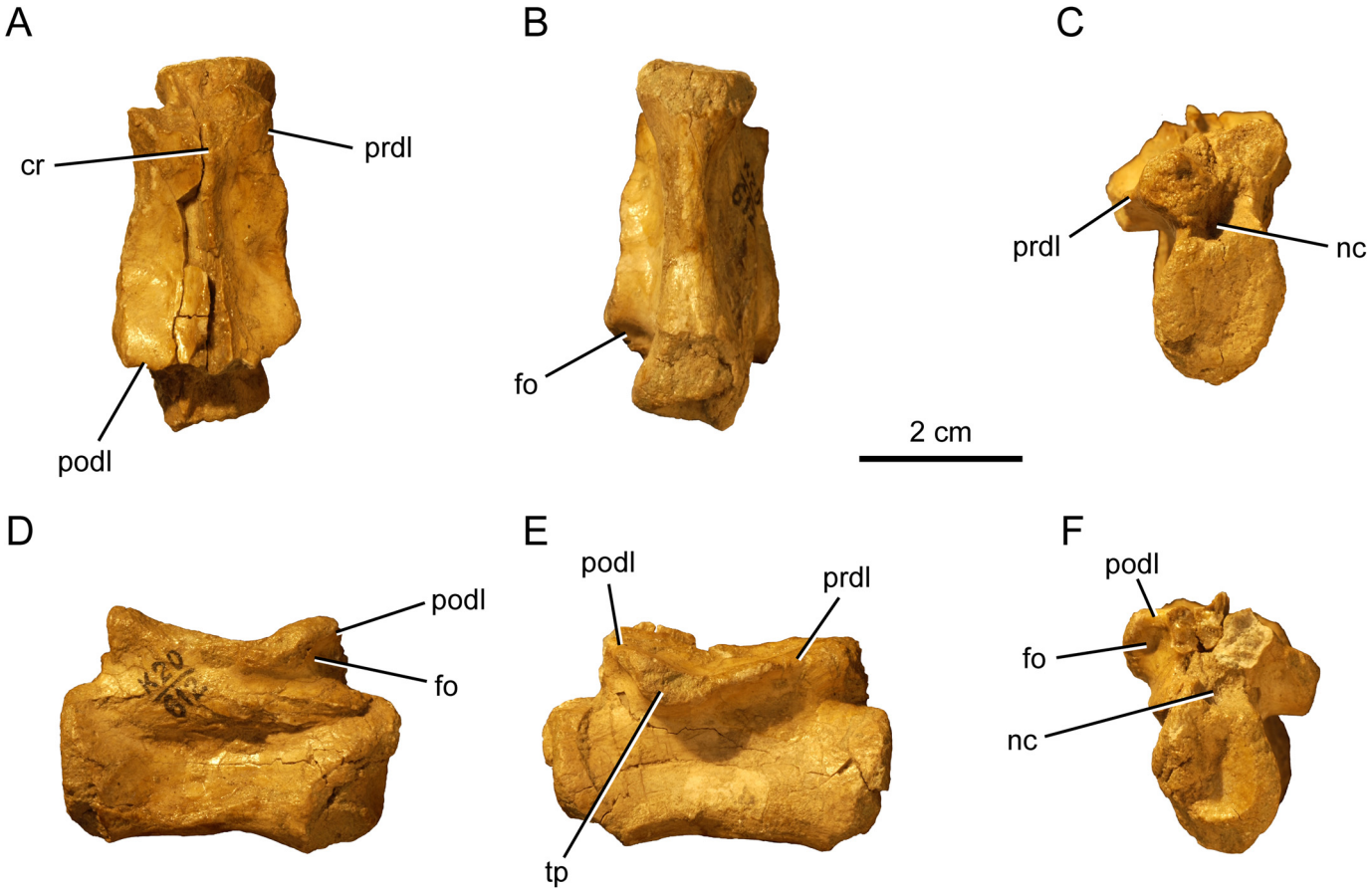

FIGURE 6. *Laevisuchus indicus* caudal vertebra GSI K20/612 in **A**, dorsal, **B**, ventral, **C**, anterior, **D**, left lateral, **E**, right lateral, and **F**, posterior views. **Abbreviations**: **cr**, crest; **fo**, fossa; **nc**, neural canal; **podl**, postzygodiapophyseal lamina; **prdl**, prezygodiapophyseal lamina; **tp**, transverse process.

4 mm) than the Meckelian groove (ca. 1 mm). Just ventral to the anterior terminus of the Meckelian groove opens a relatively large, posteriorly directed foramen. Apart from a much smaller opening positioned just posterior to it and one approximately 1 cm anterior to it, there are very few other foramina visible on the medial aspect of the dentary.

The symphyseal portion of the dentary begins just in front of the Meckelian groove. The symphysis is tipped anterodorsally with respect to the long axis of the dentary and extends from the anterior margin of the dentary to a line between the terminus of the Meckelian groove and the posterior margin of the first alveolus—essentially the area occupied by the first dentary tooth. It is featureless, apart from a prominent, circular bump positioned along the posterior margin of the symphysis. A series of fused paradental plates extends along the dorsal margin of the medial surface of the dentary. These plates bear elongate wrinkles that project anterodorsally in the same orientation as the symphysis.

The lateral aspect of the dentary is marked by numerous foramina (Fig. 7B). These do not appear to be distributed randomly on the external surface, rather they are concentrated dorsally and ventrally. Most of the foramina are small, but there are several large foramina positioned near the preserved alveolar margin of the dentary. Each opens within a small fossa and appears to be associated with an alveolus. There is a tendency for those towards the anterior end of the dentary to turn downward, possibly indicating a similar trajectory for the alveolar margin of the dentary. A conspicuous sulcus is present on the anterior margin of the external dentary (Fig. 8). It is approximately the breadth of the first tooth and anterodorsally oriented in a similar fashion. A similarly positioned sulcus is present, but developed in more pronounced fashion, in the dentary of *Masiakasaurus* (Carrano et al., 2002:fig. 3a).

Five alveoli are preserved in RTMNU/DG/VERT/1/55P/2020 (Fig. 7A). They are broken in different sectional planes, which complicates direct comparisons of their dimensions and shape (Table 1). Nevertheless, the alveoli increase in areal extent distally, with the first alveolus approximately two-thirds the size of the fourth. Broken crowns are present in the odd-numbered alveoli, and crowns 1 and 3 are broken flush with the preserved alveolar margin. Crown 5 is complete enough to observe a small portion of the mesial carina and serrations, but not complete enough to observe details of crown shape (Fig. 7A, D). There are 9 serrations visible on the 1.36 mm of carina exposed (6.6 serrations/mm). The serrations appear to be oriented perpendicular to the carina.

μCT imaging of the dentary reveals additional details about tooth orientation and the pattern of tooth replacement (Fig. 9B). There are two replacement teeth present in alveoli 1–3, and alveolus 4 bears only a single replacement tooth. Alveolus 5, which preserves a partial functional tooth, is broken away medially, and any replacement teeth that were present have been lost.

Tooth angulation is most pronounced in the first tooth, which is strongly procumbent (47°). The orientation of each tooth was

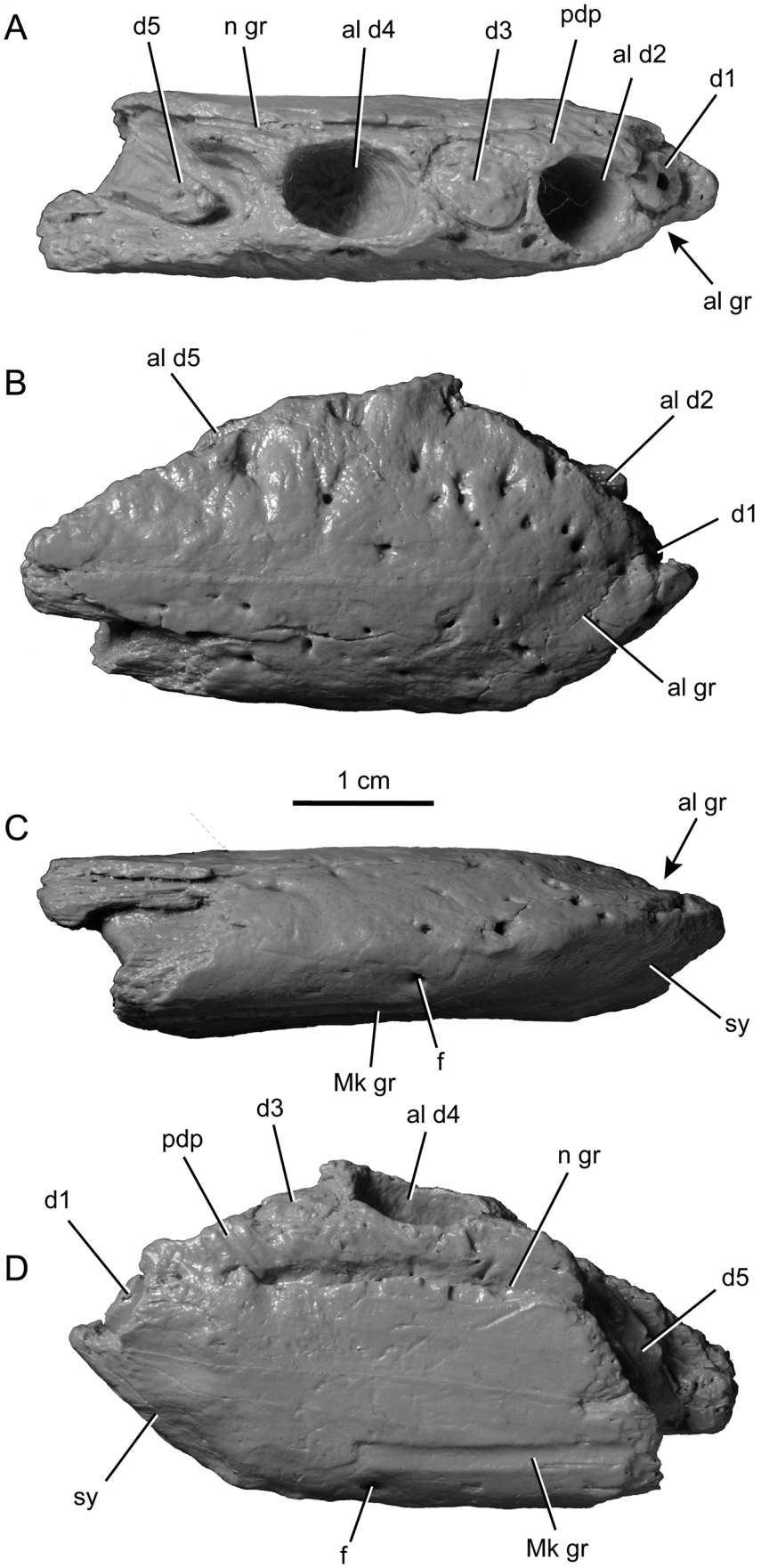

FIGURE 7. Noasauridae indet. RTMNU/DG/VERT/1/55P/2020. Photographs of a cast of the partial right dentary in **A**, dorsal, **B**, lateral, **C**, ventral, and **D**, medial views. **Abbreviations**: **al**, alveolus; **al gr**, alveolar groove; **d**, dentary tooth; **f**, foramen; **Mk gr**, Meckelian groove; **n gr**, nutrient groove; **pdp**, paradental plates; **sy**, symphysis.

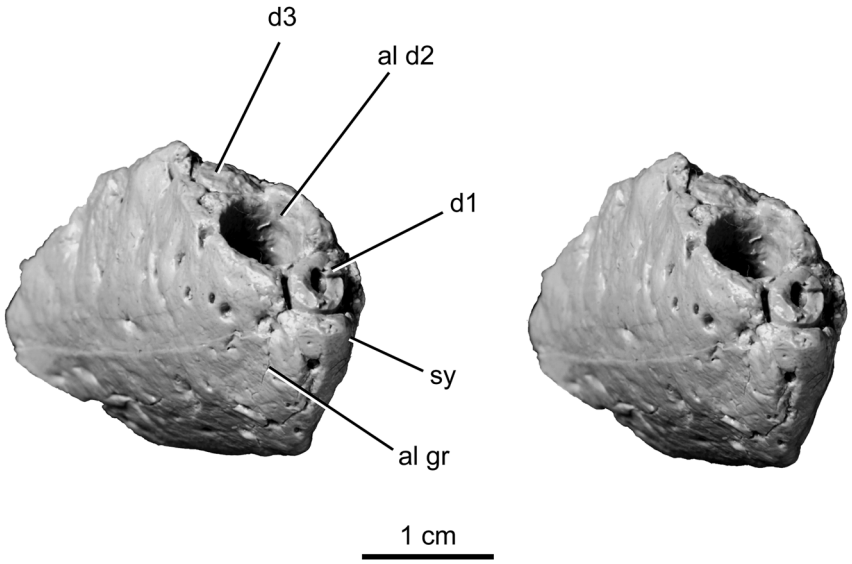

FIGURE 8. Noasauridae indet. RTMNU/DG/VERT/1/55P/2020. Stereopairs of a cast of the partial right dentary in anterior view. **Abbreviations**: **al**, alveolus; **al gr**, alveolar groove; **d**, dentary tooth; **sy**, symphysis.

measured relative to the vertical axis, established as perpendicular to the Meckelian and nutrient grooves visible on the medial side of the dentary (Table S1; Fig. 7D). Tooth 2 is slightly less procumbent, and the degree of angulation decreases steadily posteriorly, receding to just under 23° in tooth 5. Based on the rate of procumbency decrease in teeth 1–5, we extrapolate that a vertical orientation would be reached by dentary tooth position 8 or 9. Although the degree of dentary tooth angulation is less pronounced in the Indian species than in *Masiakasaurus*, based on this estimate the teeth would reach a vertical orientation in approximately the same place in the jaw. The preserved details of dentary teeth 2 and 4 in the Indian species are not sufficient to determine whether they, like those of *Masiakasaurus*, were spatulate in form. Dentary tooth 5 appears to be laterally compressed and serrated, as are dentary teeth 5–12 of *Masiakasaurus* (Carrano et al., 2002:514) and those of other abelisauroids.

The Pisdura dentary resembles in some ways that of the medium-sized Late Cretaceous abelisaurid *Niebla antiqua* (Aranciaga Rolando et al., 2021), whose dentition appears to be slightly less procumbent. The dentary of abelisaurids from India such as *Indosuchus raptorius* can be distinguished from the Pisdura dentary by their much larger size, more convex and heavily ornamented lateral surface, thicker transverse dimension, heavier and more angled symphysis, and more vertically oriented dentition (e.g., AMNH 1960, AMNH 1753).

ABELISAURIDAE Bonaparte and Novas, 1985
INDET.
"*COMPSOSUCHUS SOLUS*"
(Fig. 10)

"*Compsosuchus solus*" was based on a nearly complete axis, GSI K27/696, collected from the "Carnosaur Bed" along with *Laevisuchus* (Huene & Matley, 1933:60; pl. 20, fig. 1). Novas et al. (2004, 2010) considered "*Compsosuchus*" to be an abelisaurid lacking autapomorphies, but Carrano and Sampson (2008) hypothesized that it might be a noasaurid due to its small size and abelisauroid features.

The specimen is available in the Geological Survey of India collections and remains in the state of preservation as when it was first described by Huene and Matley (1933:pl. 20, fig. 1). The axis is nearly complete, lacking the distal tip of the odontoid, the neural spines, and parts of the postzygapophyses. Both Huene and Matley (1933:60) and Novas et al. (2004:78) interpreted this element to represent an axis fused to the atlantal intercentrum, but we interpret it to represent only the axis, with the axial intercentrum and odontoid process (atlantal pleurocentrum) firmly fused to the body of the axial pleurocentrum. There is but a single, clearly demarcated ridge wrapping underneath the element from right to left sides, which we interpret to represent the suture between axial intercentrum and pleurocentrum (Fig. 10B, C). There is no indication of a second ridge that would demarcate an additional co-ossified element. Moreover, there is no indication of an atlantal neural arch, and the positional relationships between the axial intercentrum, odontoid process, and costal articulations match those in the axes of *Majungasaurus* (O'Connor, 2007:fig. 6), *Rahiolisaurus* (ISI 658; Novas et al., 2010:fig. 3.2), and *Ceratosaurus* (Madsen & Welles, 2000:pl. 14E). The atlas (i.e., atlantal intercentrum and neural arch) of "*Compsosuchus*" would have been a separate element, as it is in the aforementioned species.

The axis of "*Compsosuchus*" is ca. 7 cm long and 4.2 cm tall. It is pneumatic, as evidenced by relatively large camellae (5 × 10 mm) exposed on the broken ventral surface of the axial pleurocentrum and pneumatopores exposed on the lateral surface of the axial pleurocentrum and neural arch (Fig. 10B, C, D). The pneumatic foramen on the axial pleurocentrum, commonly referred to as a 'pleurocoel,' sits within a teardrop-shaped fossa. Those on the neural arch open ventral and posterior to the diapophysis.

The axial intercentrum is notably broad, exceeding the width of the posterior face of the pleurocentrum as well as the span of the diapophyses (Fig. 10E). The axial intercentrum is nearly half as long as the axial pleurocentrum. In ventral view, the axial pleurocentrum is hourglass-shaped owing to a waisting at its midlength (Fig. 10B). It is not clear whether a ventral keel was present, owing to surface damage in that area. Parapophyses were not preserved, but the base of the left diapophysis is preserved. It is connected to the postzygapophysis via the postzygodiapophyseal lamina, the right and left of which expand dramatically towards the posterior end of the vertebra (Fig.

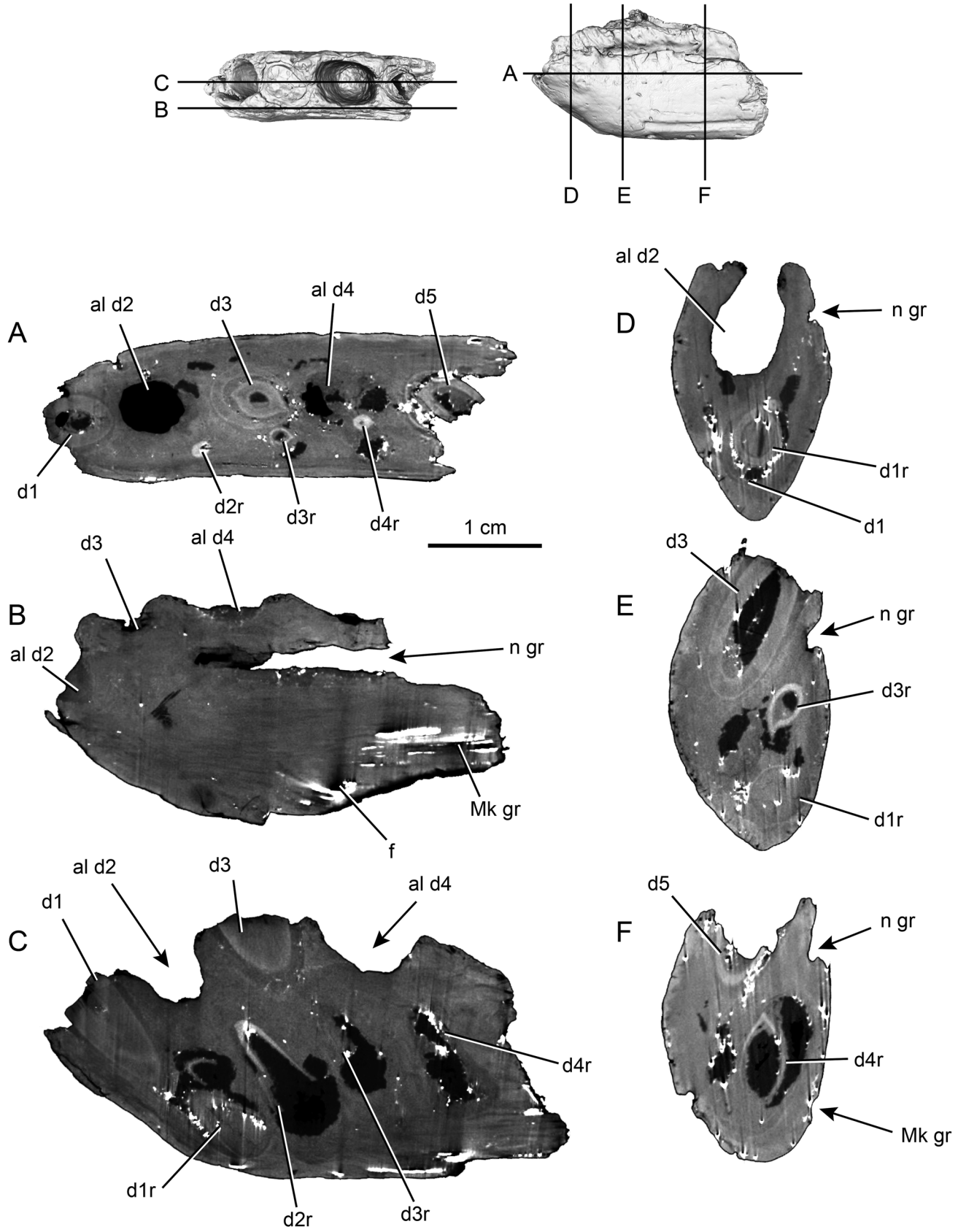

FIGURE 9. Noasauridae indet. RTMNU/DG/VERT/1/55P/2020. Computed tomography slices in the **A**, horizontal, **B**, **C**, sagittal, and transverse (**D**–**F**) planes. **Abbreviations**: **al**, alveolus; **d**, dentary tooth; **Mk gr**, Meckelian groove; **n gr**, nutrient groove; **r**, replacement tooth.

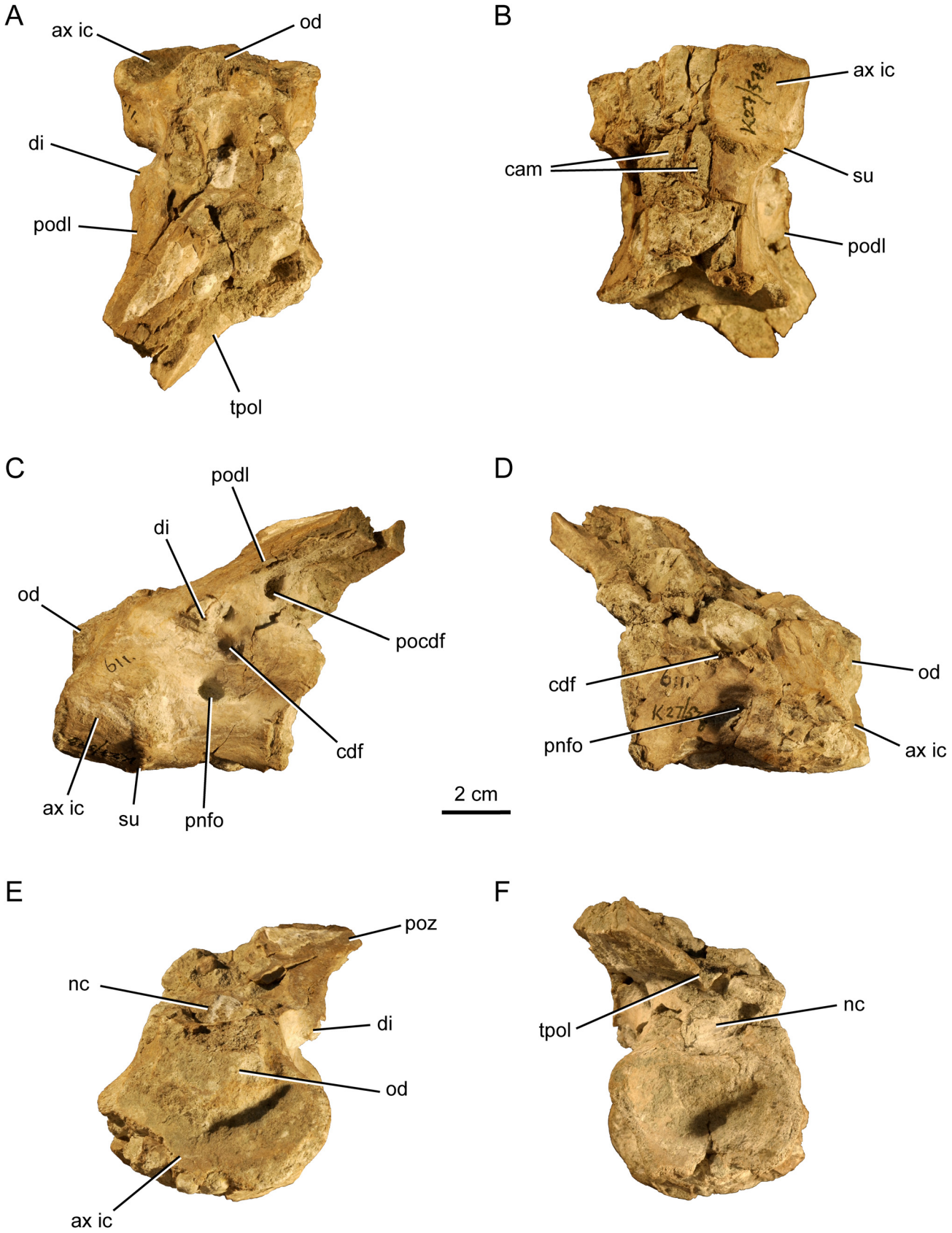

FIGURE 10. "*Compsosuchus solus*" axis GSI K27/578 in **A**, dorsal, **B**, ventral, **C**, left lateral, **D**, right lateral, **E**, anterior, and **F**, posterior views. **Abbreviations**: **ax ic**, axial intercentrum; **cam**, camellae; **cdf**, centrodiapophyseal fossa; **di**, diapophysis; **nc**, neural canal; **od**, odontoid; **pnfo**, pneumatic foramen; **pocdf**, posterior centrodiapophyseal fossa; **podl**, postzygodiapophyseal lamina; **poz**, postzygapophysis; **su**, suture; **tpol**, intrapostzygapophyseal lamina.

10A). When complete, the axial neural arch would have been triangular in dorsal view, resembling those of the abelisaurids *Rahiolisaurus* (Novas et al., 2010:fig. 3.2) and *Majungasaurus* (O'Connor, 2007:fig. 6).

The size and proportions of "*Compsosuchus*" match those of a subadult specimen of *Majungasaurus* (UA 8678; see O'Connor, 2007:table 1) and the Late Cretaceous Brazilian abelisaurid *Thanos simonattoi* (Delcourt & Iori, 2020). It also resembles the abelisaurid *Rahiolisaurus* (Novas et al., 2010), which is approximately twice as large and was collected from deposits in western India that are slightly older than those of Jabalpur and Pisdura (Wilson Mantilla et al., 2022). Méndez (2014) and Delcourt and Iori (2020) identified two features diagnosing the axis of Brachyrostra, a subgroup of abelisaurids, one of which is also present in "*Compsosuchus*": height difference between anterior and posterior axial central faces more than one half. In "*Compsosuchus*" the posterior face of the axial centrum is inclined approximately 90° relative to the horizontal, which differs from the brachyrostran condition of less than 75°. In addition to possessing a synapomorphy of brachyrostran abelisaurids, the axis of *Compsosuchus* differs from those of noasaurids. It does not resemble that of *Masiakasaurus*, the only known noasaurid axis, in the relatively broad and elongate proportions of its axial intercentrum, the relatively small diameter of its neural canal, and its posteriorly broadening neural arch (see Carrano et al. 2011:fig. 12). For these reasons, we concur with Novas et al. (2004) that "*Compsosuchus*" is an abelisaurid, rather than a noasaurid, theropod. It probably pertains to a species closer in size to *Majungasaurus* (body length 6–7 m; Sampson & Krause, 2007) than to *Masiakasaurus* (body length ca. 2 m; Carrano et al., 2011; Sampson et al., 2001). There are no unique features that we could identify to defend the validity of the species, and so we conclude that GSI K27/696 pertains to an indeterminate abelisaurid species, as previously suggested by Novas et al. (2004, 2010).

ABELISAUROIDEA Bonaparte, 1991
INDET.
"*ORNITHOMIMOIDES* (?) *BARASIMLENSISIS*"

This species is based on four vertebrae (GSI K27/541, GSI K27/531, GSI K27/604, GSI K27/682) that were considered to be dorsal vertebrae "recalling *Ornithomimus*" in their simple structure and reduced lamination (Huene & Matley, 1933:64; pl. 21, figs. 1–3). Novas et al. (2004:81) correctly identified these as caudal vertebrae and suggested they bore no autapomorphies justifying their generic or specific uniqueness. We concur with this assessment and consider these four vertebrae to represent an indeterminate abelisauroid species.

PHYLOGENETIC AFFINITIES

Novas et al. (2004:80) concluded that *Laevisuchus* more closely resembles *Noasaurus* than *Masiakasaurus*, based on "the development of pneumatic cavities, the presumed absence of neural spines on cranial cervical vertebrae, and in the position of the both [sic] pre- and postzygapophyses." Nearly all phylogenetic analyses that have included *Laevisuchus* as an OTU were unable to resolve its relationships within Noasauridae or pruned it from some or all analyses due to high levels of missing data (e.g., Brougham et al., 2020; Delcourt, 2017; Langer et al., 2019; Pol & Rauhut, 2012; Rauhut & Carrano, 2016; Sánchez-Hernández & Benton, 2014; Tortosa et al., 2014; Wang et al., 2017; Zaher et al., 2020). Using the Zaher et al. (2020) dataset but with the inclusion of an additional specimen from Australia, Poropat et al. (2020:fig. 5) resolved *Laevisuchus* as the immediate outgroup to Noasauridae, which in that analysis consisted of the sister-subfamilies Elaphrosaurinae (*Limusaurus*, *Elaphrosaurus*, Australian specimen) and Noasaurinae (*Noasaurus*, *Masiakasaurus*, *Vespersaurus*, *Velocisaurus*, *Afromimus*).

The Zaher et al. (2020) *Spectrovenator* matrix itself is based on earlier analyses by Pol and Rauhut (2012) and Rauhut and Carrano (2016). A character distribution map (Fig. S1) shows the anatomical distribution of characters within a dataset, which can indicate where the richest sources of character data are likely to reside within the skeleton (Whitlock & Wilson, 2013). The *Spectrovenator* dataset consists of approximately 43% cranial characters, nearly two-thirds of which code variation in dermal skull bones. Lower jaw characters constitute the next largest proportion of cranial characters and make up ca. 6% of total characters. Nearly one-third of the dataset consists of appendicular characters, especially those coding variation in the pelvis and hindlimb, which together account for 20% of total character data. Axial features contribute the least to the character data, representing only one-quarter of the total. Cervical vertebral characters account for more than half the axial skeleton characters; together with dorsal vertebral characters they make up 16% of all characters. We added two new characters to the Zaher et al. (2020) *Spectrovenator* matrix.

219. Groove in the anterior dentary, oriented as the teeth and positioned just posterior to the first alveolus: absent (0); present (1).
220. Orientation of mesial-most dentary teeth: (0) nearly vertical; (1) procumbent, angled at least 30° with respect to vertical.

We were able to score characters 219 and 220 for 38% and 33% of the OTUs, respectively.

In addition to the two new characters, our analysis added revised scorings for *Laevisuchus*, based on its augmented hypodigm, and the Pisdura dentary (Supplementary File 2). Zaher et al. (2020, supplementary information) were able to score *Laevisuchus* for 15/218 characters (ca. 7%). They did not score "*Jubbulpuria*" separately, nor did they include it within the *Laevisuchus* scorings. Our analysis scored six additional characters (21/220 or ca. 10%) for *Laevisuchus*, and seven characters could be scored for the Pisdura dentary (7/220 or ca. 3%).

Results

Phylogenetic analysis of *Laevisuchus* and the Pisdura dentary recovered 162,108 MPTs of 453 steps (Consistency Index: 0.523, Retention Index: 0.727). The strict consensus recovered several major nodes, including Neotheropoda, Abelisauridae, and several subgroups within Abelisauridae (Fig. 11A). There was no resolution among noasaurid taxa, all of which are in an unresolved basal polytomy that includes the two Indian OTUs. Not surprisingly, the 50% majority-rule tree preserved many more nodes, including most of the nodes within Noasauridae present in the original *Spectrovenator* analysis (Zaher et al., 2020:fig. 7). *Laevisuchus* and the Pisdura dentary were both recovered within Noasauridae. The Pisdura dentary was recovered within an unresolved clade including *Masiakasaurus*, *Velocisaurus*, and *Noasaurus*. *Laevisuchus* was recovered in an unresolved position outside that clade.

The iterative PCR script identifies taxa whose position is unstable amongst equally parsimonious trees owing to conflicting characters or missing data (Pol & Escapa, 2009). Zaher et al. (2020:suppl. info 2.4) employed iterPCR on the *Spectrovenator* dataset and identified *Laevisuchus*, *Kryptops*, *Genusaurus*, *Pycnonemosaurus*, and USNM 8415 as unstable. Our analyses, which include new characters and new scorings for Indian taxa, identified a slightly different set of unstable taxa. Eight taxa were identified as unstable: *Berberosaurus*, *Spinostropheus*, *Kryptops*, *Genusaurus*, *Pycnonemosaurus*, USNM 8415, *Laevisuchus*, and the partially resolved clade (*Rahiolisaurus*, *Aucasaurus*, *Carnotaurus*, *Daholokely*) (*Ilokelesia* (*Ekrixinatosaurus*,

Skorpiovenator)). When these OTUs are excluded from the strict consensus topology, relationships within Noasauridae are nearly fully resolved (Fig. 11B). *Noasaurus*, *Masiakasaurus*, *Velocisaurus*, and the Pisdura dentary are in an unresolved polytomy, outside of which is the clade *Limusaurus* (*Elaphrosaurus*, CCG 20011), the singleton *Deltadromeus*, and the clade *Camarillasaurus* + MNN TIG6. *Laevisuchus*, which was identified as unstable, was recovered in several alternate positions within the subgroup of Noasauridae that excludes *Camarillasaurus* + MNN TIG6.

Our results support placement of *Laevisuchus* and the Pisdura dentary within Noasauridae; the latter falling within a clade that includes *Masiakasaurus* and *Noasaurus*. Current character data available for *Laevisuchus* is not yet sufficient to resolve its affinities within Noasauridae—despite the presence of several similarities noted in the description and scored in character data. Characters that support the inclusion of *Laevisuchus* within Noasauridae are restricted to cervical vertebrae and related to the shape of the zygodiapophyseal table, the neural spine, and pneumaticity (see Table S2). Features suggesting a close relationship between *Laevisuchus* and *Masiakasaurus* are more broadly distributed among the cervical vertebrae and dorsal centrum. The Pisdura dentary shares features with *Masiakasaurus* that include the shape of the symphysis, procumbent mesial-most dentary teeth, and the presence of an alveolar groove on the lateral surface of the anterior dentary. These features have an ambiguous optimization because they could not be scored in *Noasaurus*, which thus far lacks that element.

PALEOBIOGEOGRAPHIC IMPLICATIONS

Since its earliest recognition as a distinct theropod family, Abelisauridae (Bonaparte & Novas, 1985) was cast as one of several exemplary "endemic, vicariant families (or higher taxonomic groups) that differentiated in Gondwana after the separation of this supercontinent from Laurasia around the Late

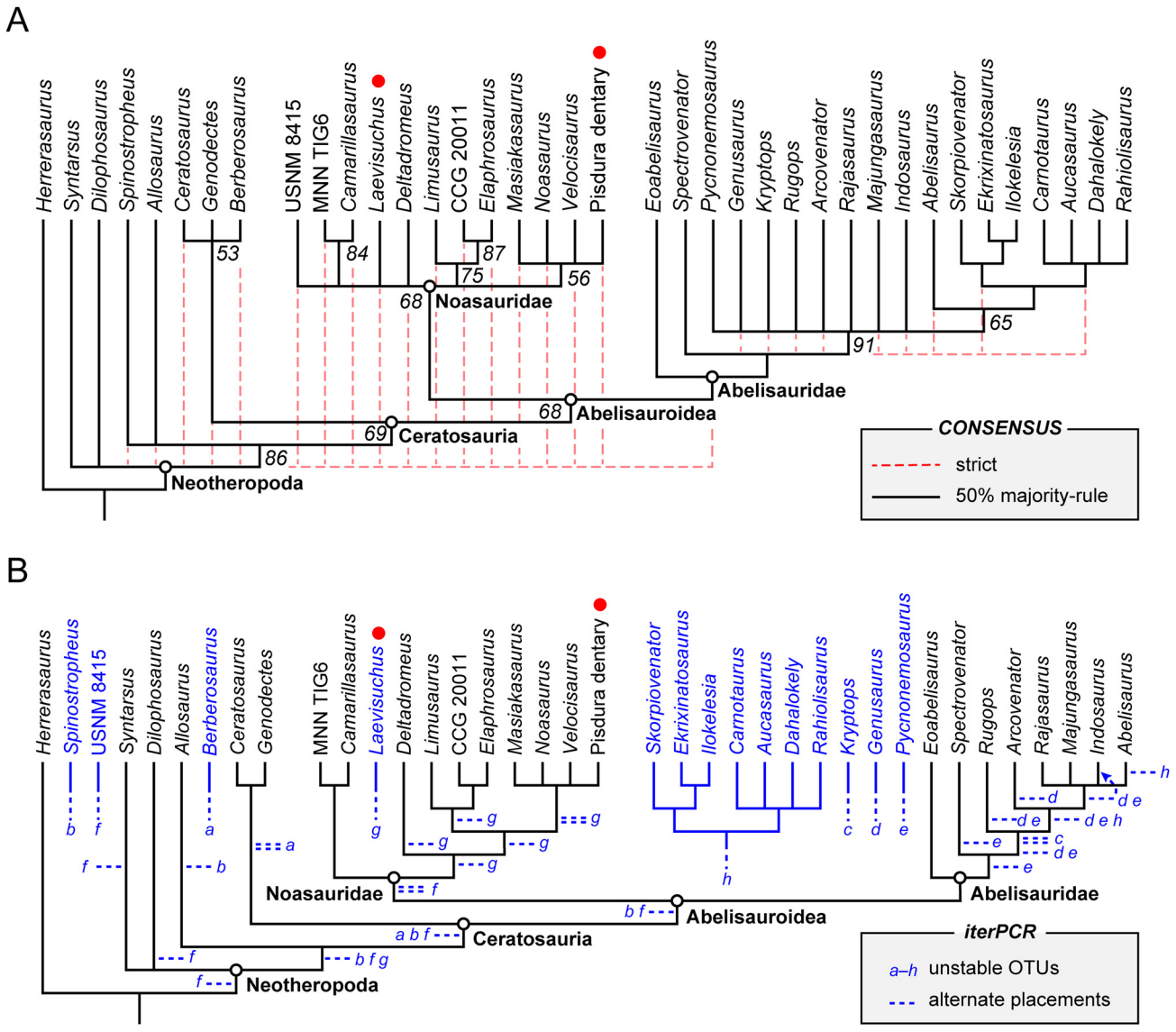

FIGURE 11. Phylogenetic analysis showing relationships among abelisauroid dinosaurs showing the inferred position of *Laevisuchus* and referred dentary RTMNU/DG/VERT/1/55P/2020 (indicated with filled circles). **A**, results of strict (dashed lines) and 50% majority-rule consensus (solid lines); italicized numbers indicate percentage of most parsimonious trees containing the designated node. **B**, results of iterPCR with unstable OTUs indicated with lighter color and labeled with an italics letter tethered to the topology on three or more alternate branches. Double dashed lines indicate alternate placements at all more distal branch segments.

Jurassic" (Bonaparte, 1986:64). At that time, Abelisauridae was understood to contain Late Cretaceous taxa from South America (*Abelisaurus*, *Carnotaurus*) and India (*Indosuchus*). Only later were taxa from the Late Cretaceous of Madagascar (*Majungasaurus*) and Europe suggested to be members of the family (Bonaparte, 1991; Buffetaut et al., 1988). Although the Late Cretaceous *Noasaurus* and the family Noasauridae had been named earlier than Abelisauridae, it was originally considered to be an aberrant monotypic coelurosaur lineage (Bonaparte & Powell, 1980). The close affinities of the families Noasauridae and Abelisauridae were first formally recognized as Abelisauroidea by Bonaparte (1991), apparently following unpublished thesis work by Fernando Novas (1989). At that time, Noasauridae included only the genus *Noasaurus*; it was not until later that Late Cretaceous Malagasy (*Masiakasaurus*) and Indian (*Laevisuchus*) taxa were recognized as members of the group (Carrano et al., 2002).

The spatiotemporal distribution of Abelisauroidea has become better defined over the last two decades, with members of the group discovered in horizons in the mid-Cretaceous of Africa (e.g., *Rugops*, Sereno et al., 2004), Early Cretaceous of Europe (e.g., *Genusaurus*, Accarie et al. 1995), and Late Jurassic of Asia (e.g., *Limusaurus*, Xu et al., 2009). Our analysis, which is based on previous studies (Pol & Rauhut, 2012; Rauhut & Carrano, 2016; Zaher et al., 2020), incorporates a broad geographic and temporal array of abelisauroids. The hypothesis of relationships (see Fig. 11) has important paleobiogeographic implications.

Although Abelisauridae is still predominantly a Late Cretaceous clade, there are Early Cretaceous and Middle Jurassic members known from South America. Abelisauridae bears a strong South America–Madagascar–India signature, but Early Cretaceous African and European forms are known, if rare. No abelisaurid from Mesozoic Asia has been identified yet. Based on the predominance of abelisaurids from South America, especially early appearing forms, it is likely that its center of origin of Abelisauridae resides in that landmass. Noasauridae, in contrast, bears a slightly different paleobiogeographic signature. Although the clade formed by the Pisdura dentary, *Masiakasaurus*, *Velocisaurus*, and *Noasaurus* also bears the South America–Madagascar–India geographic distribution and Late Cretaceous age observed for much of Abelisauridae, the remainder of Noasauridae is mixed. The sister taxon to that clade is a Late Jurassic clade hypothesized to be Asian in origin because two of its three members are from there (*Limusaurus*, CCG 20011), despite the presence of the African taxon *Elaphrosaurus*. Other unresolved noasaurids include Lower-to-mid Cretaceous African (*Deltadromeus*, MNN TIG6) and European (*Camarillasaurus*) taxa, as well as possibly a Late Jurassic North American form (USNM 8415). Because the relationships within early appearing noasaurids are not resolved, the hypothesized origin for the clade is not yet known. The absence of pre-Late Cretaceous noasaurids from South America, despite sampling of those horizons, suggests their origin must be elsewhere, perhaps in Asia or Africa—or even Madagascar or India, for which pre-Upper Cretaceous terrestrial horizons have not yet been adequately sampled.

CONCLUSIONS

New small-bodied theropod materials from the latest Cretaceous of Pisdura, central India and a reevaluation of previously collected materials from slightly younger beds at Bara Simla suggest the presence of one or more noasaurid species bearing close affinities to similar-aged forms from Madagascar (*Masiakasaurus*) and South America (*Noasaurus*). Thus far, noasaurids from the Indian Subcontinent are only known from infratrappean horizons in Pisdura and Bara Simla, deposited during C30N-C29R and C29R magnetic polarity, respectively. Noasaurids are not yet known from older C30N infratrappeans at Rahioli, younger C29R 'transitional' intertrappeans such as Naskal (see Wilson Mantilla et al., 2022), nor non-Deccan Trap-associated localities in the Cauvery Basin of southern India or the Vitakri Formation of Pakistan.

Phylogenetic analysis resolves *Laevisuchus* in an unresolved position within Noasauridae that includes earlier-appearing Asian and African forms. The ancestral area for Abelisauridae is most likely South America, based on the predominance and early age of species from that landmass. In contrast, relatively fewer South American forms are known within Noasauridae, including the eponymous *Noasaurus* and possibly *Velocisaurus*. The ancestral area of Noasauridae cannot be resolved, owing to uncertainty in the interrelationships within the group; some of the most basally diverging members of the group are from Africa, and the earliest appearing members are from Asia.

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DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

AUTHOR CONTRIBUTIONS

DMM and JAWM designed the project. DMM and BS collected stratigraphic and sedimentological data portrayed in Figure 1. DMM, BS, and JAWM conducted paleontological reconnaissance. DMM and JAWM conducted collections research and photographed specimens. KVR and JAWM analyzed the phylogenetic data. JAWM drafted the manuscript, and all authors edited the manuscript. JAWM prepared all the figures.

SUPPLEMENTARY FILES

Supplementary File 1.pdf: Table S1, alveolar procumbency in dentary of the Pisdura noasaurid (RTMNU/DG/VERT/1/55P/2020) and *Masiakasaurus knopfleri*; Table S2, character states shared between *Laevisuchus* and other noasaurid taxa; and Figure S1, character distribution map of the *Spectrovenator* dataset (Zaher et al., 2020).

Supplementary File 2.nex: data matrix used in the phylogenetic analyses (NEXUS format). Characters and state descriptions are embedded.

Supplementary File 3.tre: most parsimonious trees generated from parsimony analysis.

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